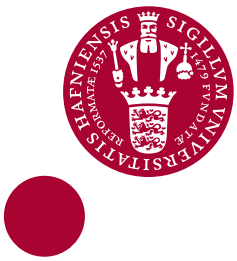

Evolution: sympatric speciation the eusocial way

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Published in:
Current biology : CB

DOI:
10.1016/j.cub.2014.07.072

Publication date:
2014

Document version
Publisher's PDF, also known as Version of record

compensatory changes, possibly involving a decrease in basal disassembly. Whether the F-actin-dependent delivery of IFT to the base of cilia is a target for various other factors known to affect length control remains to be discovered.

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http://dx.doi.org/10.1016/j.cub.2014.07.043

Evolution: Sympatric Speciation the Eusocial Way

Sympatric speciation normally requires particular conditions of ecological niche differentiation. However, ant social parasites have been suspected to arise sympatrically, because (dis)loyalty to eusocial kin-structures induces disruptive selection for dispersal and inbreeding. A new study documents this process in unprecedented detail.

**Jacobus J. Boomsma*
and David R. Nash**

In a single monumental monograph, Darwin established that competition for limited resources causes differential reproductive success and gradual adaptive change in traits for which there is heritable variation. He used these insights to deduce that all life descends from a single ancestor and that a perpetual branching process creates new lineages while others go extinct [1]. However, after the Neodarwinian synthesis starting in the 1930s, hard facts about how species originate have been accumulating slowly compared to other areas of evolutionary biology [2]. An earlier synthesis by Ernst Mayr forcefully maintained that reproductive isolation could only happen between populations that were spatially isolated, consistent with geographic distance being a universal predictor of differentiation in biological lineages [3]. Later work showed that speciation in sympatry should be possible [4] and some documented cases are now broadly accepted [5], but this alternative scenario requires unusual functional isolation between neighbouring niches to enforce mating preferences within, rather than across these niches [6–8]. A study by Rabeling *et al.* [9] published in *Current Biology* is an interesting surprise, because it represents a credible example of sympatric speciation driven by a social rather than ecological mechanism for enforcing reproductive isolation.

Rabeling and coworkers [9] studied *Mycocepurus* fungus-growing ants, including one species known to be an inquiline, *M. castrator*. Queens of such social parasites insinuate themselves into colonies of a normally closely related ant to reproduce with the help of foster workers, rather than by founding their own colonies to raise workers first. Such inquiline social parasites have evolved numerous times across multiple ant subfamilies. They are invariably rare, so their true diversity is likely to be considerably higher than presently known. The attine fungus-growing ants are a case in point, with three new inquiline species described within the last 20 years, of which *M. castrator* is the only known

inquiline in the lower attines [10–12]. The new study [9] identified the complete *Mycocepurus* species diversity in Central and South America, recovering all six known species and identifying an additional five undescribed species. The authors also monitored 17 Brazilian populations of *M. goeldii*, the host species of *M. castrator*, inferring that 16 of these were free of *M. castrator* parasites. They went on to sequence nuclear and mitochondrial genes to demonstrate that the parasite evolved less than one hundred thousand years ago, but remains more closely related to some host populations than to others, rendering the host species paraphyletic. This effect emerged most clearly for the nuclear genes, as the more rapidly evolving mitochondrial genes had already diverged more so that parasite and hosts could be interpreted as monophyletic sister lineages.

Capturing a *Mycocepurus* inquiline in the act of sympatric speciation is fortuitous in the sense of having the right team of biologists study the right ant model system in the optimal evolutionary time window, but not in the sense of being unexpected. More than a hundred years ago the Italian and Austrian entomologists Carlo Emery and Erich Wasmann independently recognized that many ant social parasites are closely related to their hosts and Alfred Buschinger has accumulated arguments for a sympatric speciation explanation of these recurrent phenomena for several decades [13,14]. The increasing availability and resolution of genetic markers thickened the plot in recent years, with several studies providing further support for inquilines evolving in sympatry [15,16], although opposing voices continued to be heard [17]. The new study by Rabeling and colleagues [9] now seems to settle the issue in the sense that we have a first eusocial case in which all relevant conditions for sympatric speciation [2,7] are demonstrated in a single study: that host and inquiline are sister-species in extant sympatry and without gene-flow, even though they have exchanged genes in the past and have speciated without being allopatric. This does not imply that all inquiline ant social parasites must necessarily have evolved sympatrically, but this scenario has gained substantial credibility, particularly for inquilines with very close resemblance to their extant host.

Why have inquiline social parasites of ants been singled out as candidates for sympatric speciation? Social parasites also occur in eusocial halictid and allodapine bees, polistine and vespine wasps and bumblebees [18]. However, these hosts tend to have semelparous colonies, so their parasites are usurpers that kill or chase away foundresses to take over incipient nests and reproduce in the same season. Of the eusocial insects with perennial colonies, only the ants have inquilines that penetrate host colonies by stealth rather than brute force and who coexist with host queens that continue to raise workers, but no longer raise reproductives from the moment inquiline reproduction starts [14]. The ants are also the only eusocial lineage in which secondary polygyny (re-adoption of newly mated daughter queens in existing nests) has evolved in appreciable frequencies [19]. Such eusocial polygyny has many advantages when it allows colonies to expand their territories and increase longevity. However, it also implies a fundamental form of social corruption, because the new queens are inseminated by unrelated males, so their offspring are less kin-selected to remain loyal to the joint reproductive interests of the chimeric colony they help maintain (Figure 1). The attine fungus-growing ants are almost universally monogynous (one queen per colony), but *M. goeldii* is an exception to this rule, just like some *Acromyrmex* species in which facultative polygyny has evolved and in whose colonies inquilines have been reported as well [10,12].

The ants evolved obligate eusociality in exclusively full-sib colonies founded by life-time monogamous parents (a single queen and her stored sperm) [20]. This major evolutionary transition turned workers into life-time altruists, comparable to somatic tissues of metazoan bodies. The later emergence of polygyny meant that these unmated workers became a public good that could be exploited by intruding genotypes, and that initially rare exploitative mutants could increase in frequency when they bred locally with other carriers of these exploitative genes [13,14,19]. It then seems rather straightforward to imagine how this can initiate the disruptive selection vortex that is typically needed for sympatric speciation to work (Figure 1). Rabeling *et al.* [9] report that *M. castrator* indeed mates in the natal nest and that its males have lost a key genital adaptation that allows mating in the air or on vegetation during dispersal flights — the normal mating system in ants including the host species *M. goeldii*. So, as soon as ant populations establish recurrent queen adoption, this creates patches of chimeric workers that are less discriminating against immigrants and offer predictable niche space for a cheater morph to specialize on. Conceptually, this is very similar to larvae of phytophagous insects colonizing an alternative sympatric host plant with many new digestive challenges to which novel adaptations can only evolve when mating becomes segregated according to host plant [5]. The difference is that those scenarios will not commit a new species to permanently low dispersal and inbreeding as is unavoidable in the eusocial scenario.

The results of Rabeling *et al.* [9] should provide a major incentive for evolutionary biologists studying ants to investigate similar host–inquiline pairs to see whether more cases can be brought to light in which mitochondrial and nuclear genes tell different stories that would be puzzling except when interpreted as evidence for sympatric speciation. Confirmation of this study in other ant lineages would vindicate the Emery/Wasmann/Buschinger model for inquiline ant evolution, but would also have wider implications for how we think about sympatric speciation. Much of the enduring controversy over the likelihood of sympatric speciation hinges on definitions, with many arguing that we should adopt non-geographic definitions and focus on actual dispersal and gene-flow to evaluate scenarios in which reproductive isolation can or cannot arise [4,6,7]. The study by Rabeling *et al.* [9] reinforces this point because the driving force in *Mycocepurus* sympatric speciation has nothing to do with geography and everything to do with novel dispersal modes and gene-flow restrictions caused by a

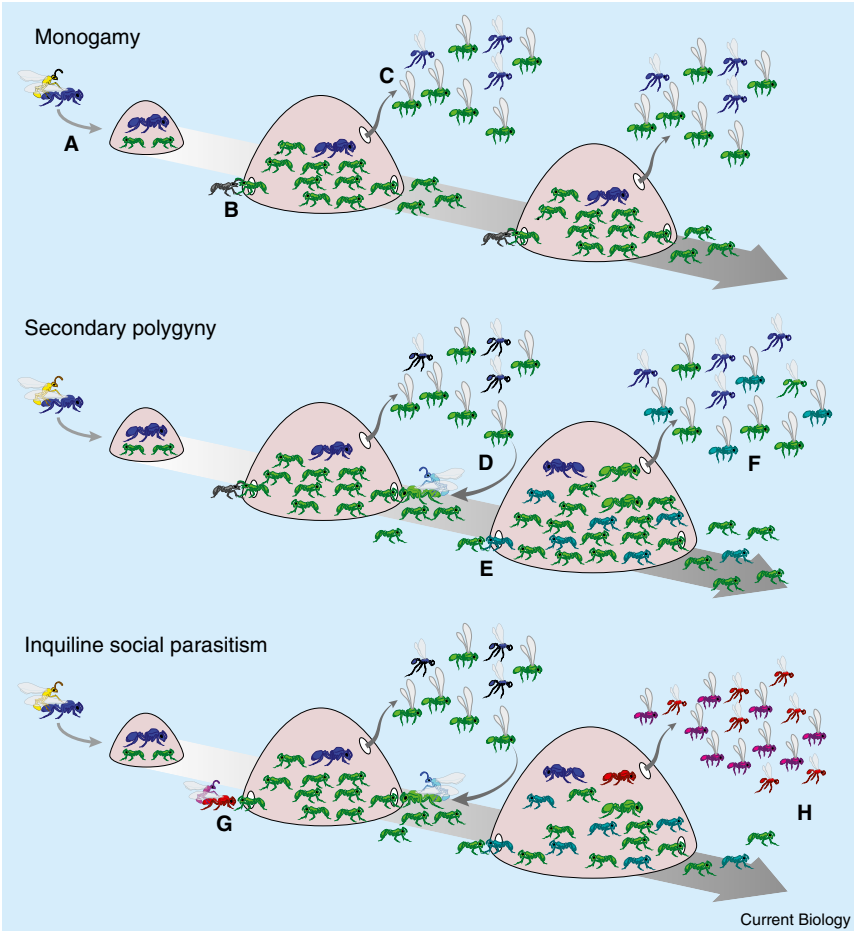

Figure 1. The hypothesized sympatric route to new inquiline ant species.

The ancestral state of all ants is monogamy (top panel), whereby a single queen founds a colony (monogyny) after having mated with a single male (A) whose sperm she stores for life. All workers are full sisters, which facilitates self/non-self discrimination, as all workers share chemical cues derived from the same genetic background and a shared nest environment (B). Workers are equally related to all workers and female reproductives produced by their mother queen, so mother and offspring both benefit from an optimal partitioning of resources into growth (more workers) and reproduction (C), although their optimal sex ratios of reproductives differ. Many ant genera have subsequently evolved secondary polygyny (middle panel), in which virgin reproductive females that have left the nest are re-admitted after having mated with less- or unrelated males (D), so that the colony obtains multiple reproductive queens. The increased genetic diversity introduced into polygynous colonies via these male genes can have many advantages in terms of protection against pathogens and colony efficiency. However, genetic chimerism also necessitates relaxed self/non-self discrimination (E) and leads to selection for 'royal cheats', as any matriline that can bias its representation in the reproductive caste, relative to the worker caste, will pass on more of its genes to subsequent generations (F). Genes coding for the exploitation of distant kin in the same nest increase by mating locally, leading to disruptive selection for local inbreeding among cheats versus dispersal and outbreeding among non-cheats. This can ultimately lead to the sympatric evolution of inquiline social parasitism (bottom panel), where there is no longer gene exchange between sister species, so the inquiline can evolve further morphological, behavioural and life-history adaptations to enhance its success in gaining access to host colonies by evading self/non-self discrimination (G). Specialization on exploiting the worker force of the host colony will then allow the inquiline to lose its own worker caste and produce only reproductives of smaller body size than those of the host (H).

fundamental change in eusocial organization. It thus appears that the creation of consistent disruptive selection for bimodal assortative mating is decisive, as originally suggested by Maynard Smith [8], regardless of the spatial distribution of the incipient species.

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http://dx.doi.org/10.1016/j.cub.2014.07.072